

Species difference in adaptive use of public information in sticklebacks

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Animals foraging on variable food sources can refine their estimates of patch quality by monitoring the success of others (i.e. collect 'public information'). Here, we show that both three-spined sticklebacks (*Gasterosteus aculeatus*) and nine-spined sticklebacks (*Pungitius pungitius*) use past cues provided by others to locate food but only nine-spined sticklebacks use prior public information to assess patch quality, regardless of whether demonstrators were conspecifics or heterospecifics. Moreover, nine-spined but not three-spined sticklebacks preferentially hid in vegetation during the demonstration, a position from which they could observe both patches simultaneously and collect public information. We conclude that species differences in the use of public information can be explained by variations in habitat choice and response to predation. Our findings expand current understanding of the scope of public-information use in animals by showing that fishes can use public-information in a foraging context and from heterospecifics. The study suggests that public-information use is an adaptation that allows animals vulnerable to predation to acquire valuable foraging information at low risk.

Keywords: public information; patch assessment; foraging; habitat partitioning; sticklebacks

1. INTRODUCTION

In a variable environment animals foraging on patchily distributed resources need to gather information about relative patch profitability before they can make an optimal choice (Giraldeau 1997). Sampling provides an individual with direct personal experience of the patch but may have associated costs such as lost feeding opportunities, travel time between patches and increased exposure to predators. While foraging with other animals may incur costs associated with competition, these costs can be reduced if foragers collect information about relative patch quality by watching others' success. This specific type of social information is called 'public information' and it provides an additional source of information to social foragers, potentially enabling more rapid and accurate assessment than through sampling alone (Valone 1989; Valone & Templeton 2002). Public information differs from other forms of information acquired through social learning in that it specifically relates to the quality of a resource rather than its location ('local enhancement') or the means ('social learning') of obtaining it (Valone 1989; Valone & Templeton 2002).

A recent review predicted that public-information use should be widespread because it potentially provides assessment benefits to individuals in a variety of social contexts (Valone & Templeton 2002). Indeed public-information use has been reported in the selection of breeding sites in birds (Doligez *et al.* 2002) and in the assessments of the relative values of mates and competitors by fishes (Nordell & Valone 1998; McGregor *et al.* 2001). However, there are grounds for suspecting that

public-information use in a foraging context requires more sophisticated cognition than that in a mate-choice or agonistic context, because the former but not the latter requires individuals to assess the relative profitability of resources that are typically separated in time and space, based solely on the successes of others, whereas the latter alone can exploit cues that directly indicate the relative value of the resources (e.g. fleeing and chasing). Consistent with this assessment, reports of public-information use in a foraging context have so far been restricted to birds (see Templeton & Giraldeau 1995, 1996; Smith *et al.* 1999). In addition, all work so far has examined public-information use by conspecifics, and demonstrating that public-information use can be extended to heterospecifics would expand its potential scope.

In this study we investigated whether two species of fish, three-spined and nine-spined sticklebacks, use public information in a foraging context and whether they can exploit public information provided by heterospecifics. These fishes occur sympatrically in small streams, have rather similar diets (FitzGerald & Wootton 1996) and regularly forage in mixed-species shoals. Recent work using two sympatric species of fish reports shoaling preferences for familiar heterospecifics over non-familiar conspecifics (Ward *et al.* 2003). The natural co-occurrence of three-spined and nine-spined sticklebacks may promote public-information use among heterospecifics.

2. MATERIAL AND METHODS

(a) *Fishes and holding conditions*

We used 86 three-spined sticklebacks (mean \pm s.e. size of 32.23 ± 0.82 mm) and 86 nine-spined sticklebacks (mean \pm s.e. size of 32.18 ± 0.93 mm). All fishes were collected in a stream in Histon near Cambridge, UK. Both populations were kept in

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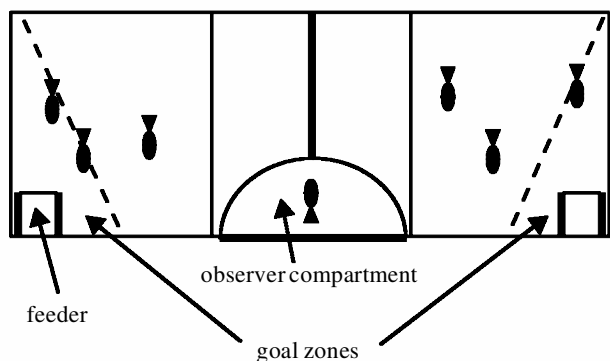


Figure 1. Diagram of the experimental-tank set-up for experiments 1–3 during the observation period. Thick lines represent opaque partitions, thin lines represent transparent partitions and dashed lines represent goal zone delimitations.

tanks at a water temperature of 10–14 °C and fed on frozen bloodworms. Testing occurred in spring 2002 (experiments 1–3) and February 2003 (experiment 4). Because the motivation to reproduce affects fish behaviour (Pitcher 1996), we took measures to limit the interference of breeding state. Tests were interspersed in such a way that no experiment was conducted earlier in the breeding season than the others and fishes were kept on a stable 12L : 12D cycle. The 36 h of food deprivation experienced by the fishes before testing almost certainly generated a motivation to feed sufficient to inhibit any reproductive behaviour.

(b) *Experimental protocol*

Fishes spent at least 12 h (including overnight) in the experimental tank on the day preceding their testing to reduce possible exploratory behaviour during the test (Mikheev & Andreev 1993). Observers were then placed in a holding tank until testing.

The experimental tank (90 cm × 30 cm, 18 cm water level) was divided into three sections of equal size. Prior to introducing the fishes, the experimenters (I.C. for experiments 1–3 and Y.v.B. for experiment 4) installed the partitions as shown in figure 1 and figure 4a and placed opaque partitions along the goal-zone delimitations to prevent the demonstrators from interacting with the feeders before the start of the experiment. Half a transparent plastic bottle of diameter 21 cm and height 22 cm served as the observer compartment, placed in the central section of the tank. Two groups of demonstrators, consisting of three fishes each, were placed in the end sections of the tank. Demonstration was provided by conspecifics in experiments 1, 2 and 4 and by heterospecifics in experiment 3. The observer was then placed in the observer compartment and all fishes were allowed to settle for 10 min (see figure 1 and figure 4a). The removal of the opaque partitions in front of the feeders marked the beginning of the observation period, which lasted for 10 min. On the 'rich' side of the tank, two to three bloodworms in water were delivered at 90 s and every 90 s after that, i.e. six times during the observation period. The 'poor' side either received no food at all (experiment 1) or received two to three bloodworms at 90 s and 360 s, i.e. twice during the observation period (all other experiments). The feeders were 25 cm high columns with opaque sides facing the observer but a transparent front facing the demonstrators, who would peck at the bloodworms as they sank to the bottom of the column, where they were eaten through a slot. This design prolonged the demonstration,

making it a salient cue for the observer. Whenever food was delivered to the feeder on the 'rich' side only, a similar amount of water and bloodworm juice (water in which the bloodworms had been defrosted) was delivered to the feeder on the 'poor' side to control for any movement of the feeder and for possible residual chemical cues on the 'rich' side. For each experiment, patch status was randomly assigned in a balanced way so that the 'rich' patch was presented 10 times on the left side and 10 times on the right side of the tank. In all experiments the observer fish was unable to see the food directly, and was required to make judgements about the profitabilities of the patches solely on the basis of the foraging success of the demonstrators.

At the end of the observation period, the observer was visually isolated from the rest of the tank by opaque partitions placed around the central section, and the demonstrators and any remaining bloodworms were removed. Hence, the only type of information that observers had about patch quality at the moment of choice was prior public information. The observer was then allowed to swim freely in the central section for *ca.* 5 min. A black plastic hide was pulled in front of the tank, concealing the experimenter and laboratory surroundings from the observer fish, to avoid any biasing of the fish's decision by cues other than prior demonstration. All partitions in the tank were then removed and the testing period started. The test continued until the observer penetrated a goal zone ('poor' or 'rich') or until 90 s had elapsed after the observer left the central section, whichever occurred last.

(c) *Behavioural data and statistical analysis*

During the testing period, the position of the fish was scanned 10 times per minute (i.e. every 6 s). We considered a fish to be in a zone when its body up to the pectoral fins was in that zone. Because the fish's choice as to which side it preferred was clearer when in either goal zone than when in either zone adjacent to the central section, we focused our analysis on the use of the goal zones only. We compared for each species the proportion of fishes that entered the 'rich' goal zone first with expected values at random (half the fishes) using χ^2 -tests. Then we compared the mean per cent time a fish spent in each goal zone using paired *t*-tests. In order to compare the two species in their goal zone preferences, we combined the time spent in each goal zone for each species and tested for species differences through the interaction term (species × zone use). We used ranked data to deal with non-normality (Potvin & Roff 1993).

During the demonstration period of experiment 4, we recorded every 15 s whether the focal fish was in or out of cover. We calculated the proportion of scans in which the focal fish was seen in cover for each species. Cover represented *ca.* 25% of the central section of the tank. We compared the values for the two species using an independent-sample *t*-test, and compared them with random expectation based on cover area (i.e. 25%) using paired *t*-tests for each species.

3. RESULTS AND DISCUSSION

(a) *Experiment 1: conspecific demonstrators feeding on a food versus no-food schedule*

In experiment 1, we simply tested whether observers were able to use cues given off by feeding conspecifics to locate a single patch delivering food, despite the absence of food and of knowledgeable demonstrator fishes at the moment of choice. This is a less challenging task than

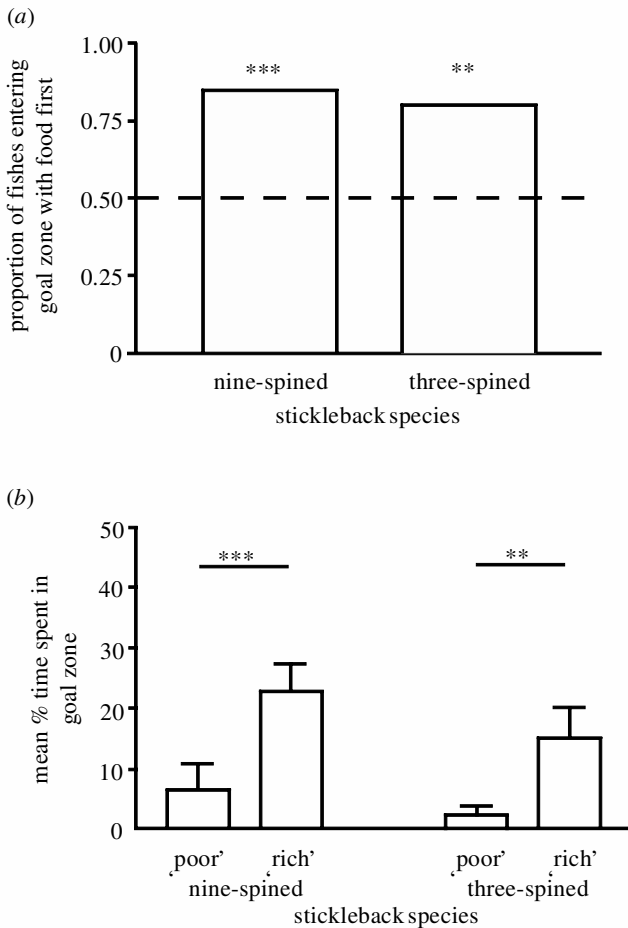


Figure 2. Observers' behaviour after a demonstration of conspecifics feeding on a food versus no-food schedule. (a) Proportion of nine- and three-spined stickleback observers that entered the goal zone that previously contained the 'rich' patch first ($n = 20$ for each species). The dashed line indicates the proportion expected at random. (b) Mean (\pm s.e.) per cent time nine- and three-spined stickleback observers spent in each goal zone ($n = 20$ for each species). ** $p < 0.01$, *** $p < 0.005$.

public-information use, and may be reliant on a process known as 'delayed local enhancement'. We found that observers of both species did pay attention to the feeding fishes in one patch and used the information derived from them to determine the location of food (Boyd & Richerson 1988; McQuoid & Galef 1992; Day *et al.* 2003). Indeed, 17 out of the 20 tested nine-spined stickleback observers ($\chi^2_1 = 9.79$, $p = 0.002$) and 16 out of the 20 tested three-spined stickleback observers ($\chi^2_1 = 7.19$, $p = 0.007$) first entered the goal zone that had previously delivered food (figure 2a). In addition, observers of both species spent significantly more time in the goal zone that had previously contained feeding demonstrators (the 'rich' patch) than in the one that had contained fishes non-feeding (the 'poor' patch) (nine-spined: $t_{19} = -3.88$, $p = 0.001$; three-spined: $t_{19} = -3.03$, $p = 0.007$; figure 2b). The two species showed no difference in the proportion of fishes that chose the 'rich' goal zone first ($\chi^2_1 = 0.39$, $p = 0.53$) nor in their relative use of the 'rich' goal zone (ANCOVAR, species \times zone use: $F_{1,38} = 0.64$, $p = 0.43$), suggesting that the two species can equally well collect information regarding food location without sampling for themselves.

It is unlikely that the prior location of food was indicated to the observer fish by residual olfactory cues from the 'rich' patch, both because sticklebacks predominantly hunt by sight and have been reported to have a relatively poor sense of smell (Honkanen & Ekstrom 1992), and because water with a bloodworm flavour was delivered on the 'poor' side whenever food was delivered on the 'rich' side. While observers were tested shortly after the observation period had ended, the findings nonetheless demonstrate some memory component in the choice (Milinski 1994). The fact that food was concealed from the observers during the observation period by opaque sides to the feeders confirms that behavioural cues from conspecifics can suffice to generate differential attraction to food patches (Krause 1992), which is a prerequisite for public-information use.

(b) Experiment 2: conspecific demonstrators feeding on a rich versus poor schedule

In a second experiment, using a similar procedure, observers watched two equal-sized groups of conspecifics feeding on patches that delivered food at two different rates, and were subsequently tested to see whether they had acquired a preference for the patch with the higher profitability. Given that both patches delivered food, the important component of the information relates here to patch quality rather than location alone.

Nine-spined sticklebacks exhibited a significant preference for the more profitable patch with 16 out of the 20 tested observers visiting the 'rich' patch first ($\chi^2_1 = 7.19$, $p = 0.007$; figure 3a). Moreover, these subjects spent significantly more time in the goal zone of the 'rich' patch than in that of the 'poor' patch ($t_{19} = -3.19$, $p = 0.005$; figure 3b). These results suggest that nine-spined sticklebacks can use prior public information provided by conspecifics.

Three-spined sticklebacks exhibited no patch preference, with 10 out of the 20 tested fishes entering the 'rich' goal zone first ($\chi^2_1 = 0$, $p = 1$; figure 3a), and no preference evident in the use of goal zone ($t_{19} = 0.32$, $p = 0.76$; figure 3b). A higher proportion of nine-spined than three-spined sticklebacks entered the 'rich' goal zone first ($\chi^2_1 = 7.19$, $p = 0.007$), and nine-spined sticklebacks spent relatively more time in the 'rich' goal zone (ANCOVAR, species \times zone use: $F_{1,38} = 5.74$, $p = 0.022$). These findings suggest a species difference in the use of public information, and that three-spined sticklebacks either could not discriminate the difference in quality between the 'rich' and the 'poor' patches or did not use this information to exploit their environment.

Krause (1992) reports that three-spined sticklebacks are more attracted to fishes feeding at a higher food delivery rate than an otherwise equivalent group feeding at a lower rate, but that they no longer show differential attraction to the site once the feeding period is over. This suggests that three-spined sticklebacks can discriminate between two levels of excitement or relative success of feeding fishes but that, once feeding conspecifics are removed, the information is not subsequently used to prefer the richer patch. Our results are in accordance with previous empirical work on three-spined sticklebacks that hints at their need to sample physically to assess relative patch quality (Gotceitas & Colgan 1991).

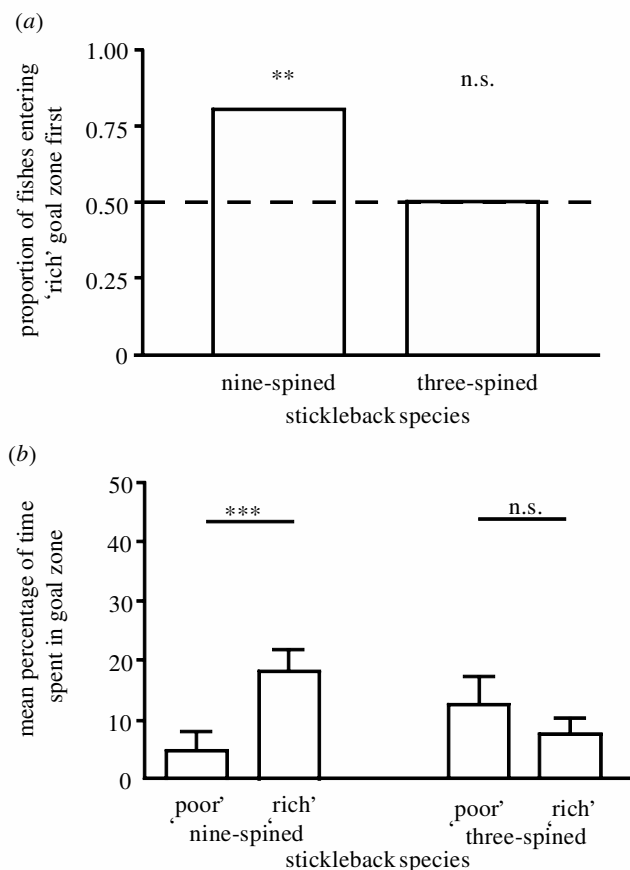


Figure 3. Observers' behaviour after a demonstration of conspecifics feeding on a 'rich' versus 'poor' schedule. (a) Proportions of nine- and three-spined stickleback observers that entered the goal zone of the 'rich' patch first ($n = 20$ for each species). The dashed line indicates the proportion expected at random. (b) Mean (\pm s.e.) per cent time nine- and three-spined stickleback observers spent in each goal zone ($n = 20$ for each species). ** $p < 0.01$, *** $p < 0.005$; n.s., not significant.

(c) Experiment 3: heterospecific demonstrators feeding on a rich versus poor schedule

Here, we replicated experiment 2 but with heterospecific demonstrators, in order to address the alternative hypothesis that the observed species difference reflected a difference in the quality of demonstration. Moreover, as three-spined and nine-spined sticklebacks are often sympatric, these species are ideal to test whether individuals can use public information obtained from heterospecifics.

Once again, nine-spined sticklebacks showed a greater preference for the 'rich' patch than three-spined sticklebacks. When comparing the two species, it appears that a greater proportion of nine-spined sticklebacks entered the 'rich' goal zone first ($\chi^2_1 = 5.0$, $p = 0.025$) and overall they spent more time in the 'rich' than in the 'poor' goal zone (ANOVAR, species \times zone use: $F_{1,38} = 5.60$, $p = 0.023$) compared with three-spined sticklebacks. Nine-spined sticklebacks showed a significant preference for the 'rich' patch, with 15 out of the 20 tested observers visiting the 'rich' patch first ($\chi^2_1 = 5.0$, $p = 0.025$). Moreover, nine-spined sticklebacks showed a significantly higher use of the goal zone of the 'rich' patch (29.03 ± 5.76 per cent time) than of that of the 'poor' patch (5.93 ± 2.60 per cent time) ($t_{19} = -2.86$, $p = 0.01$). The fact that nine-spined

sticklebacks used public information derived from heterospecifics could be the result of the close ecology of the two species in terms of habitat and diet. However, it could equally imply that individuals capable of using public information from conspecifics can also use cues provided by heterospecifics, whether closely related or not. The sources of information that animals use to guide their choices may thus be wider than hitherto suspected. Although we know of cases of local enhancement being driven by heterospecific cues (e.g. Whiting & Greeff 1999), our results show for the first time, to our knowledge, that heterospecific cues can serve in assessing patch quality.

Three-spined stickleback observers failed to show a preference for either patch, with 10 out of the 20 fishes visiting the 'rich' patch first ($\chi^2_1 = 0$, $p = 1$), and no evidence of a preference for the 'rich' goal zone ('rich': 5.16 ± 1.78 per cent time; 'poor': 11.95 ± 4.49 per cent time; $t_{19} = 0.46$, $p = 0.65$). These results suggest that three-spined sticklebacks did not use prior public information provided by nine-spined demonstrators.

The fact that the results followed the same pattern as experiment 2 clearly shows that the difference in performance between species is not rooted in the quality of the demonstration but rather in some characteristic of the observing individuals. This confirms the findings of experiment 2 suggesting that nine-spined sticklebacks do, and three-spined sticklebacks do not, use public information.

Nine-spined and three-spined sticklebacks exhibit subtle habitat partitioning (FitzGerald & Wootton 1996; Hart 2003), which may generate different opportunities to observe from afar. Recent empirical work (Hart 2003) shows that solitary nine-spined sticklebacks use weeded areas more than three-spined sticklebacks, even when food is present only in the open water. Three-spined sticklebacks may thus join a group of feeding fishes upon detection and trade their opportunities to watch from afar with physical sampling. Conversely, nine-spined sticklebacks may stay at a distance for some time before deciding to leave cover, and natural selection may have favoured the use of this time to collect public information. This hypothesis will hold only if nine-spined sticklebacks remain in cover while companion fishes forage in the open. We tested this with a fourth experiment.

(d) Experiment 4: access to cover for observers during demonstrations

Here, we replicated experiment 2 but with the observer fish no longer constrained in an observer compartment. The subject was free to move anywhere in the central section of the tank and was provided with natural vegetation as cover from which it could observe the demonstration (figure 4a).

Consistent with our hypothesis, nine-spined stickleback observers spent significantly more time in cover than three-spined sticklebacks ($t_{19} = -4.36$, $p < 0.001$; figure 4b), and more time in cover than would be expected by chance ($t_{19} = -5.14$, $p < 0.001$). In comparison, three-spined sticklebacks did not use cover differently from chance expectation ($t_{19} = 0.35$, $p = 0.73$; figure 4b). However, three-spined sticklebacks did not appear to attend both demonstrations equally. Rather, the more time they

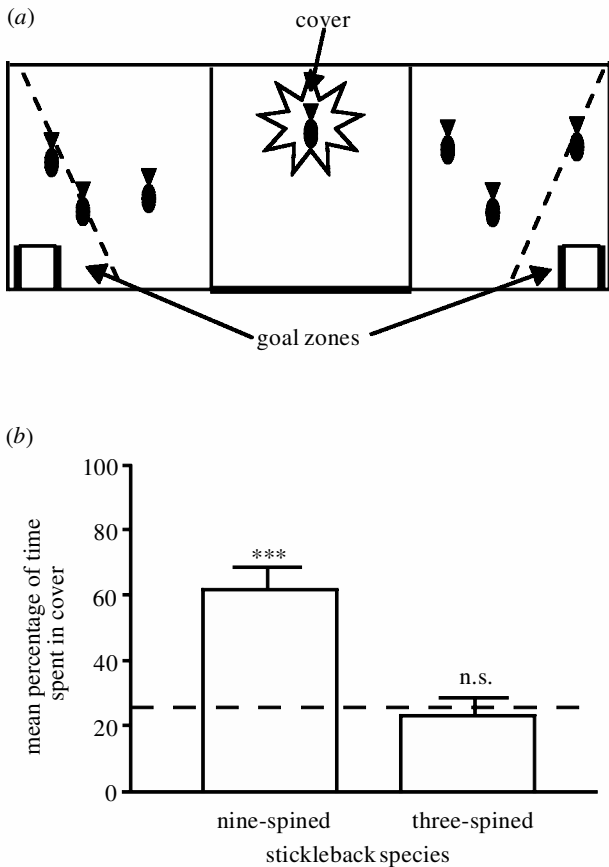


Figure 4. (a) Diagram of the experimental-tank set-up for experiment 4 during the observation period (see legend to figure 1 for details). (b) Mean (\pm s.e.) per cent time nine- and three-spined stickleback observers spent in cover during the demonstration period ($n = 20$ for each species). *** $p < 0.005$; n.s., not significant.

spent near one group of demonstrators, say the 'poor' side, the less time they spent near the other group ($r = -0.747$, $p < 0.001$), suggesting that they mostly attended one or the other demonstration and thus obtained only partial information. Such partial information may be enough to discriminate between patch values when only the 'rich' option delivers food (experiment 1), but probably not when both options are rewarded (experiments 2–4).

When tested for a preference after the demonstration, nine-spined sticklebacks spent more time in the 'rich' goal zone relative to the 'poor' goal zone (ANOVAR, species \times zone use: $F_{1,38} = 6.36$, $p = 0.016$) and a higher proportion of fishes entered the 'rich' goal zone first ($\chi^2_1 = 7.27$, $p = 0.007$), compared with three-spined sticklebacks. Nine-spined sticklebacks again spent more time in the 'rich' goal zone (32.7 ± 6.5 per cent time) than in the 'poor' goal zone (4.5 ± 2.1 per cent time) ($t_{19} = -4.44$, $p < 0.001$) and 15 fishes out of 20 entered the 'rich' goal zone first ($\chi^2_1 = 5.0$, $p = 0.025$). Three-spined sticklebacks again failed to show a preference for either goal zone ('poor': 15.7 ± 6.2 per cent time; 'rich': 19.4 ± 7.3 per cent time; $t_{19} = 0.17$, $p = 0.87$) and only nine out of 20 fishes entered the 'rich' goal zone first ($\chi^2_1 = 0.2$, $p = 0.66$). These results support the hypothesis that nine-spined sticklebacks use time in cover to observe feeding events from afar and thereby collect public information. By con-

trast, three-spined sticklebacks do not use cover more than expected by chance and seem to favour physical over visual sampling.

Combining the findings for three-spined sticklebacks from experiments 2–4, a power analysis using the effect size found for this species in experiment 1 gives a power of 0.9 (using the methods recommended by Cohen (1988)). Thus we can be confident that the failure of three-spined fishes to exhibit behaviour consistent with public-information use is not caused by the sample size.

4. GENERAL DISCUSSION

The consistent preference of nine-spined sticklebacks for the richer patch in experiments 2–4 strongly suggests that these fishes are capable of using public information. Conversely, the consistent absence of a corresponding choice in three-spined sticklebacks, in spite of the high power of the analyses, suggests that this species employs a different strategy in social foraging.

These findings are likely to be of interest for three reasons. First, we provide original evidence that fishes can use public information to assess foraging-patch quality. The use of public information requires animals to make a judgement as to the relative profitability of resources on the basis of the success of others, an ability that many researchers have assumed requires sophisticated cognition. It is perhaps surprising that this ability is observed in a species not hitherto noted for its intelligence.

Second, the fact that two closely related species differ in their social foraging strategies suggests a compelling example of adaptation to local resources. It allows us to dismiss the notion that public-information use is a relatively trivial ability, and implies that this character will covary with features of life history and habitat use rather than intelligence. This is consistent with the fact that the use of public information is reported in some (Templeton & Giraldeau 1995, 1996; Smith *et al.* 1999) but not other (Valone & Giraldeau 1993; Smith *et al.* 2001) species of passeriform birds. The abilities of visual assessment and its incorporation in the information-gathering and decision-making processes are thus probably driven by ecological rather than taxonomic determinants. We present experimental evidence supporting our hypothesis that this species difference is rooted in a subtle difference in habitat use.

Third, this is the first time, to our knowledge, that the use of public information obtained from heterospecifics has been demonstrated in any animal species, and in any context. Our study strongly supports Valone & Templeton's (2002) prediction that public-information use is more widespread among animals than previously thought.

We dismiss the counter-argument that the process underlying the nine-spined sticklebacks' patch choice was social attraction, based on differences in the excitement of the demonstrators during the observation period. Social attraction should have been greater in the 'rich' patch than in the 'poor' patch, irrespective of whether the 'poor' patch delivered less food than the 'rich' patch or failed to deliver any, but three-spined sticklebacks showed a preference for the 'rich' patch in experiment 1 only.

Neither do we consider the preference of three-spined sticklebacks for the patch delivering food over that

delivering none in experiment 1 as satisfactory evidence for public-information use in that species. The fact that, in three other experiments dealing with a difference in patch quality, three-spined sticklebacks showed no patch preference suggests that they employ a different strategy from nine-spined sticklebacks in the discrimination of patch quality. Although, at first sight, the distinction between local enhancement and public information (Valone 1989; Valone & Templeton 2002) may seem subtle, it is likely that the latter is associated with substantially more complex cognition than the former. Our finding that three-spined sticklebacks chose the 'rich' patch in local-enhancement situations but not in public-information situations is consistent with such a distinction. This is also consistent with previous studies that suggest that three-spined sticklebacks rely on physical sampling (Gotceitas & Colgan 1991), that is, on their own feeding rate (Milinski 1984), for their final decision as to which patch to feed in.

The species difference reported in this study may reflect the better protection afforded by the larger spines and presence of armoured pelvic girdle and plates of three-spined sticklebacks compared with nine-spined sticklebacks (FitzGerald & Wootton 1996). Piscivorous fishes have been shown to attack nine-spined sticklebacks in preference to three-spined sticklebacks (Hoogland *et al.* 1957). Although both species should benefit from the use of public information, the costs and benefits of obtaining this type of information probably differ between species. The better structural defences of three-spined sticklebacks leading to their possible lower predation risk when in the open potentially allow them to cope with increased exposure to predators and to join conspecifics upon detection of a patch. In this manner, three-spined sticklebacks minimize lost feeding opportunities, which releases them from the need to collect public information. By contrast, the more vulnerable nine-spined sticklebacks appear willing to forgo the immediate opportunity to join feeding conspecifics in favour of increased safety and better assessment of patch quality through the use of public information. The experiments illustrate how two closely related and sympatric species of stickleback solve the problem of the adaptive trade-off between anti-predatory behaviour and foraging in two different ways, with only the nine-spined stickleback reliant on public information.

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